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MINI-REVIEW

Microbial communities in large-scale wood piles and their effects on wood quality and the environment

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Abstract The demand of renewable energy sources, i.e. biomass, is steadily increasing worldwide to reduce the need of fossil energy sources. Biomass such as energy crops, woody species, forestry and agricultural residues are the most common renewable energy sources. Due to uneven demand for wood fuel, the material is mostly stored outdoors in chip piles or as logs until utilisation. Storage of biomass is accompanied by chemical, physical and biological processes which can significantly reduce the fuel quality. However, heating plants require high-quality biomass to ensure efficient operation, thereby minimising maintenance costs. Therefore, optimised storage conditions and duration times for chipped wood and tree logs have to be found. This paper aims at reviewing available knowledge on the pathways of microbial effects on stored woody biomass and on investigations of the fungal and bacterial community structure and identity. Moreover, potential functions of microorganisms present in wood chip piles and logs are discussed in terms of (1) reduction of fuel quality, (2) catalysing self-ignition processes, and (3) constituting health risk and unfriendly work environment.

Keywords Bacteria · Fuel quality · Fungi · Self-ignition · Storage · Wood piles

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Introduction/economic background

The demand of renewable energy sources increased in the last decades enormously in the European Union, Canada, Russia, USA and also in other countries. This increase is possibly due to changes in the energy policy, which are based on the scope to reduce the global emission of greenhouse gases (DOE 2007; Nitsch 2008), threats of nuclear energy (Bedane et al. 2011) and of catastrophic wildfires (Evans and Finkral 2009) and also by decrease of nationally imported gas and other fossil fuels (Durant et al. 2011). Main renewable energy sources are biomass, biogas, hydropower, wind and geothermal energy, solar collectors and photovoltaics. In European countries and the USA today, energy derived from biomass is by far the most important renewable energy source (Purohit et al. 2006), and its economic importance is expected to increase rapidly in the near future (DOE 2007; Nitsch 2008). Moreover, renewable energy sources in developing countries used for household energy needs as well as for process heat production for biomass-based industries are the main energy source (Parikka 2004). The use of biomass for energy supply is presently estimated between approximately 2 and 10 % of the global net primary production (Smeets et al. 2007; IEA 2011), and it is planned in many countries as prospective bridging technology to reduce the impact of fossil energy sources and to enable the development of innovative renewable energy sources and energy storage systems (Divya and Ostergaard 2009). The most common types of biomass to generate heat energy and electricity are globally ranked as energy crops, woody species, forestry and agricultural residues, organic waste from industry, humans and animals (Fischer and Schrattenholzer 2001; Klass 1988). However, the sources and utilisation of biomass varies in different regions and countries tremendously, and wood is the most prominent biomass resource in many non-equator countries.

Forests represent approximately 27 % of the world's land area, and wood is the predominant commercial product from forests. Global wood consumption is around 3,500 million m^3 per year, and has increased by more than 65 % since 1960 (Martínez et al. 2005). Energy end-users of forest products are the industrial and commercial sectors mainly in the generation of heat and power. To use forest products as renewable energy source, the biomass will be (1) harvested, (2) piled or bundled, (3) transported and logistically processed, (4) stored, (5) comminuted, (6) upgraded through further processing to optimise fuel quality (e.g. torrefaction or pelletization) and, finally, burned. The order of the procedure differs widely depending on region and company workflow. Harvesting techniques of forest products (Anerud and Jirjis 2011) and various machines such as pelletization technologies (Zamorano et al. 2011) and mobile mechanical screening tools (Spinelli et al. 2011) have been recently optimised to support the application of wood as renewable energy source. Innovation of technical supplier underlines the economical value of industrial-scale usage. In addition, the demand of renewable energy sources caused expansion of mainly regional companies and created new jobs mostly in the forest sector (Viana et al. 2010). Forest residues and ready-to-use wood chips are piled in large-scale and usually stored outside mostly without any coverage on solid surfaces such as concrete (Noll et al. 2010b). In such piles, physical, chemical and microbiological processes that take place can affect fuel quality. This review aims at providing an overview of literature dealing with such processes, with a special focus on microbial communities present in wood chip piles as summarised in Fig. 1. However, degradation of dead wood by arthropods, molluscs, birds or other vertebrates, their bacterial symbionts and the consequences for biodiversity conservation are excluded from this review as it has been previously reviewed in detail (Breznak and Brune 1994; Kurz et al. 2008; Mattson and Addy 1975; Grove 2002; Lonsdale et al. 2008).

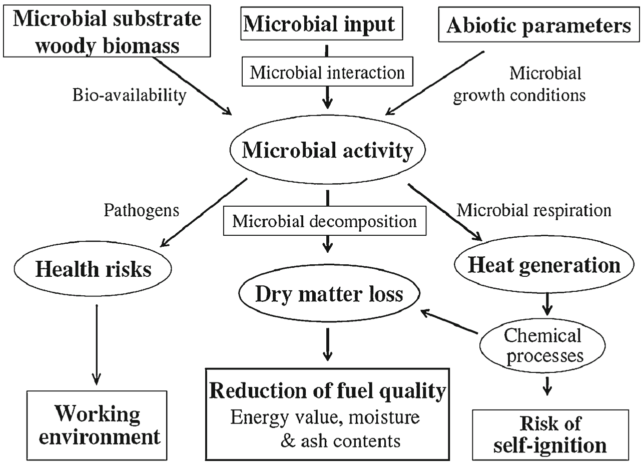

Fig. 1 A scheme showing key parameters for microbial activity, problems caused by this activity, its consequences on fuel quality and potential risks associated with storage of wood chips in large piles

Storage of woody biomass

Numerous research studies dealing with various storage methods for wood chips have been carried out. Physical and chemical properties of wood chips before and after storage as well as microbial decomposition have been assessed to evaluate the effect of storage on wood quality (Ernstson et al. 1991; Bedane et al. 2011; Casal et al. 2010). To evaluate storage impact on fuel quality parameters such as heating value, ash composition, moisture content, percentage of fine particles, slagging/fouling indices and the combustion profiles obtained from thermogravimetric analysis were analysed (Casal et al. 2010). Factors that alter the energetic quality of stored wood chips have been characterised as (1) particle size and comminution method (Scholz et al. 2005; Nati et al. 2010; Zamorano et al. 2011); (2) tree species composition (Röser et al. 2011; Scholz et al. 2005); (3) geometries of the piles (Ferrero et al. 2011); (4) geographical location (Röser et al. 2011); (5) methods for piling such as covered, compacted or ventilated (Jirjis 1995a, b); (6) time of storage (Noll et al. 2010b; Ferrero et al. 2009); (7) moisture content during piling (Filbakk et al. 2011; Bedane et al. 2011); (8) storage season (Brand et al. 2011); and (9) microbial decomposition of stored wooden biomass (see Table 1). The most important factor affecting the quality of wood as a fuel is mainly attributed to moisture content of wood (Filbakk et al. 2011; Bedane et al. 2011; Lyons et al. 1985; Jirjis 1995c). Other factors such as the heating value and ash content of the respective tree species (Röser et al. 2011; Scholz et al. 2005), the particle size distribution and homogeneity (Jirjis 2005; Scholz et al. 2005) and impurities and contaminants (Tame et al. 2007) can also to a lesser extent affect fuel quality. Storage of wood chips in piles leads to redistribution of the moisture which results in a wet outer surface and much more drier inner part (Bedane et al. 2011; Filbakk et al. 2011; Noll et al. 2010b), and therefore geometry of the pile with reduced surface area should be preferred to obtain higher wood quality. The storage time of biomass is highly dependent on both supply and utilisation and varies between few days to several months and in few cases up to years. It is often recommended to follow the strategy first in–first out to avoid high dry matter loss. Thörnqvist and Jirjis (1990) reported that the highest dry matter losses takes place during the early stages of storage (Thörnqvist and Jirjis 1990). Storage of chipped logging residues of soft wood and oak stem wood chips in compacted piles affected fungal growth negatively, compared to uncompacted storage (Jirjis 1989). However, compacting outdoor-stored chip piles is not advisable since it

Table 1 Composition of microbial communities present in stored woody biomass

Country	Type of wood; storage time (days)	Phylogenetic affiliation to fungal and bacterial genera or higher taxonomic levels[a]	Functional traits of the community members[b]	Type of analyses[c]	Reference
Sweden	Pine and spruce logging residue, chipped oak stem wood; 180 days	A: *Aspergillus fumigatus*, *Aspergillus niger*, *Aurobasidium pullulans*, *Cladosporium cladosporiodes*, *Paecilomyces varioti*, *Penicillium brevicompactum*, *Penicillium expansum*, *Penicillium* spp., *Talaromyces becilosporus*, *Trichoderma viride*	Moulds, soft-rot, potential pathogenic fungi	Culturing and microscopic counting chamber	Jirjis (1989)
Finland	Spruce, pine, birch and aspen logs	A: *Bisporella*, *Candida*, *Capronia*, *Hypoxylon*, *Lachnum*, *Leptodontidium*, *Phialocephala*, *Phialophora*, *Sympoventuria* B: *Amylostereum*, *Antrodia*, *Armillaria*, *Coniophora*, *Exidia*, *Fomes*, *Fomitopsis*, *Gymnopilus*, *Hypoderma*, *Lentinellus*, *Phellinus*, *Pleurotus*, *Postia*, *Veluticeps*	Blue-stain fungi, brown-, humus- and white-rot, potential pathogenic fungi	DGGE, cloning and sequencing and microscopic observation	Rajala et al. (2010a)
Sweden	Spruce wood debris in forest sites	B: *Amphinema*, *Antrodia*, *Athelia*, *Athelopsis*, *Boidinia*, *Botryobasidium*, *Botryohypochnus*, *Ceraceomyces*, *Conferticium*, *Coniophora*, *Corticium*, *Cylindrobasidium*, *Cystostereum*, *Dichostereum*, *Fibulomyces*, *Fomitopsis*, *Galzinia*, *Globulicium*, *Gloeophyllum*, *Gloeoporus*, *Heterobasidion*, *Hydrabasidium*, *Hypochnicium*, *Hyphoderma*, *Hyphodontia*, *Ischnoderma*, *Jaapia*, *Junghuhnia*, *Laurilia*, *Leptoporus*, *Leptosporomyces*, *Merulicium*, *Oligoporus*, *Peniophora*, *Phanerochaete*, *Phellinus*, *Phlebia*, *Phlebiella*, *Phlebiopsis*, *Piloderma*, *Resinicium*, *Serpula*, *Sistotrema*, *Sistotremastrum*, *Skeletocutis*, *Sphaerobasidium*, *Stereum*, *Thanatephorus*, *Tomentella*, *Tomentellopsis*, *Trechispora*, *Trichaptum*, *Tubulicrinis*, *Tylospora*, *Veluticeps*, *Vesiculomyces*	Brown, humus- and white-rot	Microscopic observation	Olsson et al. (2011)
Germany	Chipped pine wood; 302 days	A: *Aspergillus fusarium*, *Hormonema*, *Trichoderma* B: *Sphaeopsis*, *Cadophora*, *Rhodotorula*, *Sistotremastrum*, *Polyporales* (order) Ba: *Acidocella*, *Acidobactera* (phylum), *Caulobacter*, *Luteibacter*, *Novosphigobium*, *Pseudomonas*	Brown, humus- and white-rot, diazotrophs	T-RFLP, cloning and sequencing	Noll et al. (2010b)
USA	Maple wood chips and big red food; 4 days	A: *Aspergillus*, *Candida*, *Geotrichum*, *Hamigera*, *Neurospora*, *Penicillium*, *Pichia* Z: *Backusella*, *Mucoraceae*	Potential pathogenic fungi	F-ARISA, cloning and sequencing	Hansgate et al. (2005)
Canada	Biosolids from a wastewater treatment plant; 730 days	A: *Arthrobotrys*, *Nectria*, *Scedosporium*, *Thermomyces* B: *Conocybe*, *Coprinus*, *Cryptococcus* Ba: *Acidobactera* (phylum), *Actinomadura*, *Adhaeribacter*, *Aeromonas*, *Bacillus*, *Brevibacillus*, *Brumimicrobium*, *Byssovorax*, *Chloroflexi* (phylum), *Clostridium*, *Geobacillus*, *Hyphomonas*, *Methylocaldum*, *Microbispora*, *Microtetraspora*, *Parachlamydia*, *Pseudoxanthomonas*, *Symbiobacterium*, *Tatlockia*, *Thauera*, *Thermobacter*, *Thermoleophilum*, *Thermus*, *Thioalkalivibrio*, *Thiobacillus*, *Thiobacter*, *Thermodesulfovibrio*, TM7 (phylum), *Xanthobacter* Z: *Mortierella*	Brown- and white-rot; methanotrophic, methylotrophic, diazotrophic and denitrifying bacteria; cellulose/cellobiose and xylan degrading bacteria; potential pathogenic bacteria	DGGE, cloning and sequencing	Novinscak et al. (2009)

Table 1 (continued)

Country	Type of wood; storage time (days)	Phylogenetic affiliation to fungal and bacterial genera or higher taxonomic levels[a]	Functional traits of the community members[b]	Type of analyses[c]	Reference
China	*Keteleeria* tree logs	Ba: *Acidobacteria* (phylum), *Actinobacteria* (phylum), alpha-, beta-, gamma- and *Deltaproteobacteria* (phylum), *Bacillus*, *Bradyrhizobium*, *Burkholderia*, *Chloroflexi* (phylum), *Enterobacter*, *Frankia*, *Hydrogenophaga*, *Mycobacterium*, *Myxobacterium*, *Myxococcus*, *Paenibacillus*, *Parachlyamydia*, *Pseudomonas*, *Rhizobium*, *Verrucomicrobia*	Methylotrophic and diazotrophic bacteria; cellulose-degrading bacteria; potential pathogenic bacteria	Cloning and sequencing	Zhang et al. (2008)
UK	Green waste as windrow, 7 days	Ba: *Acidobactera* (phylum), *Agrococcus*, *Alcaligenes*, *Alkaliflexus*, *Alkalispirillum*, *Arthrobacter*, *Azoarcus*, *Bacillus*, *Brevibacillus*, *Chryseobacterium*, *Clostridium*, *Desulfitobacterium*, *Geobacillus*, *Lactobacillus*, *Oerskovia*, *Pseudoclavibacter*, *Rhizobium*, *Sphingobacterium*, *Thermobispora*, *Thermoactinomyces*	Diazotrophs; cellobiose and xylan degrading bacteria; potential pathogenic bacteria	DGGE, cloning and sequencing	(Adams and Frostick 2009)
Sweden	Spruce logs in a forest site	A: *Amphisphaeriaceae*, *Ascocoryne*, *Candida*, *Capronia*, *Cenococcum*, *Chalara*, *Chloridium*, *Cladosporium*, *Dactylella*, *Gyromitra*, *Haplographium*, *Heliotales* (order), *Holwaya*, *Hyaloscypha*, *Hymenoscyphus*, *Lecythphora*, *Leptodontidium*, *Nectria*, *Orbilia*, *Ophiostoma*, *Penicillum*, *Phialocephala*, *Phialophora*, *Sordariomycetes*, *Sporothrix*, *Scytalidium*, *Trichoderma*, *Xenochalara*, *Xylariaceae* (family) B: *Antrodia*, *Atehlia*, *Botryobasidium*, *Calocera*, *Diplomitoporus*, *Hypoderma*, *Pachnocybe*, *Phlebiella postia*, *Resinicium*, *Rhodotorula*, *Sistotrema*, *Skeletocutis*, *Tremiscus*, *Tricaptum*, *Tubulicrinis*, *Xeromphalina* Z: *Mucor*, *Mortierella*	Potential pathogenic fungi	Culturing fungi, cloning and sequencing	Lindner et al. (2011)
Germany	Chipped willow and pine wood	A: *Absida*, *Aspergillus*, *Botrytis*, *Cladosporium*, *Eurotium*, *Emericella*, *Paecilomyces*, *Penicillium*, *Rhizomucor*, *Rhizopus*	Potential pathogenic fungi	Culturing fungi	Scholz et al. (2005)

[a] Abbreviations in the column are: *A* ascomycetes, *B* basidiomycetes, *Ba* bacteria, *Z* zygomycetes

[b] Abbreviations in the column are: *brown rot*, wood-decaying species causing brown rot; *humus*, litter- and humus-decaying species; *white rot*, wood-decaying species causing white rot; *diazotrophs*, atmospheric N_2-fixing microorganisms

[c] *DGGE* denaturing gradient gel electrophoresis, *F-ARISA* fungal-automated rRNA intergenic spacer analysis, *T-RFLP* terminal restriction fragment length polymorphism analysis

can lead to heat accumulation especially in piles containing needles and bark such as logging residues.

Wood is composed of three main macromolecular components; cellulose, hemicellulose and lignin, which are present in all woods (Fengel and Wegener 1984). The relative proportion of these components is variable within tree species and can range for cellulose between 28 and 50 %; hemicelluloses, 20 and 30 %; and for lignin, 18 and 30 % relative mass fraction (Fengel and Wegener 1984). Significant variations in the concentration of these components can also be found within the same tree species (Kenney et al. 1990). Higher heating values for lignin, relative to cellulose and hemicellulose, were reported by many authors (Kollman 1951; Baker 1983; White 1987). Kollman (1951) reported that the range of effective heating value for cellulose is 17.4–18.2 MJ/kg, while lignin has 25.54 MJ/kg (Kollman 1951). Consequently, wood species with higher cellulose contents, such as *Salix* and *Populus*, have relatively low heating values (Kollman 1951). The higher heating value is directly related to the elemental composition of the wood. Susott et al. (1975) and Tillman (1978) found a linear relationship between higher heating value and carbon content. The higher heating values for lignin and cellulose are consistent with their carbon content. Therefore, selective microbial degradation of these compounds can, in addition to causing matter losses, change energy contents of the stored biomass.

Input of microbial diversity in stored woody biomass

While physical and chemical properties of wood chips have been analysed in detail, the phylogenetic community composition and the microbial activity within wood chips piles are less investigated and therefore wood logs have been included in this review. Moreover, the published studies of microbial communities in wood chip piles and wood logs can be regarded as case studies rather than large statistical analyses. This is mainly due to their large-scale (Ferrero et al. 2009), inadequate sampling strategies (Lindner et al. 2011), and the multi-parametric setups (Noll et al. 2010b) more likely case studies rather than large statistical analyses. Therefore, universally valid statements of the composition and function of a defined microbial community present in wood chips piles is difficult up to now. Nevertheless, a broad fungal and bacterial diversity was found in wood chip piles and wood logs as summarised in Table 1 and its composition is highly variable indicating that the origin of the diversity and their ability to settle and survive differed largely. Origin of microbial communities in wood chip piles and wood logs are (1) surface area of wood particles (e.g. microorganisms present on and in bark, needles or leaves), (2) previous microbial colonisation of inner parts of wood (e.g. tunnelling bacteria and wood-rotting fungi transported by arthropods or other vertebrates), (3) atmospheric deposition by rain, (4) transportation into the wood chip piles and wood logs by wind, or (5) active microbial immigration from nearby environments such as the belowground. Origin of microbial communities may differ between wood chip piles and wood logs as the composition of the microbial community in the published studies was significantly different from each other (see Table 1). The particle size of the stored biomass, as well as particle size distribution, plays a major role in the microbial establishment and growth. Chipping or crushing forest residues or other woody biomass, especially freshly harvested material, damage plant cells and release its soluble contents. The enhanced accessibility of substrates in comminuted wood chips compared to wood logs may explain shifts in microbial community composition. Moreover, the comminution process greatly increases the surface area of the biomass which facilitates extensive colonisation.

Healthy tissues of almost all wood species are hosts of endophytic fungi (Sieber 2007). Species composition of endophytic community differs among tissue types (leaves, bark and wood) and the phase disposition (age) of tissues. However, the diversity of endophytic fungi as revealed by culture-dependent methods was high but dominated by few species indicating that these dominant species are not host- or site-specific (Ahlich and Sieber 1996; Unterseher et al. 2007). The majority of endophytic fungi are Ascomycota (Caroll 1988), and they are not known to be the key players in saprotrophic degradation of wood (see also details below). However, once the host is felled and its biomass is stored as logs or wood chips, endophytic fungi are forced to resume growth, degrade the present host biomass (e.g. needles or leaves) and sporulate to infect the next host plant tissues (Sieber 2007). Therefore, the very early stage of wood colonisation after tree felling is affiliated to a high abundance of endophytic fungi which will be replaced thereafter by specialised saprotrophic microorganisms and insects. Another group of Ascomycota and Deuteromycota are known as blue-staining fungi. These fungi, most frequently attack pine sapwood, were occasionally found in chipped pine wood debris (Noll et al. 2010b) and are known to cause non-significant loss in wood quality but affect its colour.

To avoid the serious problems encountered during storage of wood chip in piles, logging residues, normally including tree top and branches (slash), can with advantage be stored without comminution in windrows. Numerous storage trials conducted in Northern Europe provided valuable information concerning fuel quality after storage in small heaps, in windrows with and without cover and in bundled units (Jirjis and Lehtikangas 1991; Filbakk et al. 2011; Jirjis and Norden 2005). A study dealing with storage of uncomminuted logging residues (Norway spruce) in 4-m-high windrows showed moderate growth of fungi and the average dry matter loss was only 1 % month^{-1} (dry weight basis) after 5 months of storage (Jirjis and Lehtikangas 1991). The same study also showed that covering the top of the windrow with impregnated paper further reduced dry matter losses to only 0.2 % month^{-1}. The estimated loss of needles during storage in windrows was marginal since the detached needles were embedded inside the windrow and did not fall through the windrow to forest floor. On the other hand, storing slash in smaller heaps during a summer season allowed the loss of the majority of the needle fraction. Needles and also leaves are in general richer in macro- and microelements compared to the respective stems and therefore needles and leaves will serve as additional substrate source for microbial colonisation of stored wood. The low substance losses during storage in windrows together with a marked reduction in the average moisture content from 42 to 21 % (wet basis) resulted in a higher total energy content after storage (Jirjis and Lehtikangas 1991). Bundling forest residues into a "composite residue log" form provides a unit that can be handled and stored more efficiently; and, moreover, results in less dry matter loss compared to chips storage (Jirjis and Norden, 2005). A more recent study, investigating storage of bundled logging residues in a pile, reported a mass loss of 1–3 % month-1 during storage. The study did not attempt to distinguish between losses caused by microbial decomposition and loss resulting from falling/detachment of needles during storage (Filbakk et al. 2011).

Functional traits of the microbial community present in stored woody biomass

Storage of woody biomass is a multi factorial environment that determines the presence and activity of the microbial community. Even wood decomposition studied at laboratory-scale revealed non-uniform decomposition patterns (Wang et al. 2011), and therefore universal decomposition patterns in wood chips and logs are unlikely. A broad variety of functional traits of the microbial community in wood chip piles and wood logs can be found (Table 1), and the decomposers of the main wood compounds are white- and brown-rot fungi (Rajala et al. 2010a, b; Noll et al. 2010b). White-rot fungi degrade mainly lignin, and at a lower rate also hemicellulose and cellulose, while brown- and soft-rot fungi remove cellulose and leave lignin essentially unchanged (Schwarze 2007). The early stage of fungal attack by the majority of brown- and some white-rot fungi occurs at a distance from the fungal hyphae by excretion of non-enzymatic low molecular weight compounds (Arantes et al. 2011). These compounds mediate by brown-rots the Fenton reaction, which involves a low molecular weight Fe^{3+} reductant to generate OH radicals; and is also of advantage for lignin peroxidase-deficient white-rot fungi (Arantes and Milagres 2007). However, the majority of white-rot fungi involve complex degradation pathways including diverse key enzyme families, which were reviewed in detail previously (Hatakka 1994; Leonowicz et al. 1999; Martínez et al. 2005). The majority of ligninolytic fungi produce freely diffusible extracellular oxidative enzymes such as lignin peroxidase, manganese-dependent peroxidase, and laccase. Lignin degradation solely by bacteria appears to be negligible in aerobic terrestrial environments compared to the activity of white-rot fungi (Tuomela et al. 2001; Kirk and Farrell 1987).

Cellulose and hemicellulose can be degraded by a broad spectrum of fungi and bacteria. However, bacterial degradation of cellulose in wood appears to be only important under wet and often anaerobic conditions and this is a very slow process (Lynd et al. 2002). Two types of bacterial wood decomposition have been distinguished by microscopic observations of wet wood namely tunnelling and erosion bacteria (Daniel 2003), and both types probably degrade cellulose (Daniel 2003). However, the importance of such cellulose-degrading bacteria in wood under fungal decay is questionable as cellulose degradation by fungi is far more rapid and efficient (Lynd et al. 2002). Rajala et al. (2010b) showed on RNA level, which fungal genera are metabolically active during wood decomposition of Norway spruce logs. Significant shifts in the active fungal community were obtained along the wood decomposition and the relative proportion of the functional diversity such as white- and brown-rot fungi also tremendously shifted. Therefore, microbial wood degradation is a highly complex process which involves a broad spectrum of different fungal species which may also have complementary functions. In addition to fungal dominance in wood decomposition, bacterial members of the genera *Adhaeribacter*, *Aeromonas*, *Byssovorax*, *Myxobacterium* and *Oerskovia* were also found in stored wood (Novinscak et al. 2009). A number of studies have shown that these bacteria are able to hydrolyse cellulose and/or cellobiose (Weon et al. 2010; Martínez-Murcia et al. 2008; Reichenbach et al. 2006). Moreover, if cellulose or cellobiose is directly available in soil excluding wood matrices, bacterial cellulose degradation takes place at either oxic or anoxic conditions (Schellenberger et al. 2010). Members of the bacterial genera *Actinomadura*, *Microbispora*, *Microtetraspora* and *Sphingobacterium* were also found in similar environments to wood chip piles (Novinscak et al. 2009; Adams and Frostick 2009) and were able to degrade hemicellulose compounds, e.g. xylan, under aerobic conditions (Holtz et al. 1991; Berens et al. 1996; Pankratov et al. 2007).

Cellulolytic fungi and bacteria exude endoglucanases, exoglucanases and β-glucosidases that act synergistically in the conversion of cellulose to glucose (Lynd et al. 2002;

Mansfield and Meder 2003). Fungal and bacterial cellulases belong to different enzyme families suggesting convergent evolution towards the same substrate specificity (Lynd et al. 2002). Thus, although components of the celluloytic system of bacteria and fungi are not closely related, their functionality is quite similar.

As fungi are superior in metabolising the main compounds of wood, the major energy sources for bacteria and non-rotting fungi in wood chip piles and logs are supposed to be sugars, starch, pectin, extractives and easy accessible cellulose (Boddy 2001). For instance, members of the fungal genus *Bisporella* were found in wood debris, which are known to be specialists in the initial stage of decomposition of cut wood irrespectively of the type of tree species (Rajala et al. 2010a). Moreover, in that study, also members of the fungal genus *Capronia* were found to be able to utilise casamino acids, casein and lipids but not cellulose, lignin or chitin (Untereiner and Malloch 1999). However, such substrate sources, that are easily accessible for the bacterial and fungal non-rotter community in wood, are present only in low amounts and therefore the supply of additional carbon sources is essential. Nevertheless, bacteria have been found to be present during fungal wood decay (Greaves 1971; Clausen 1996; Kulháková et al. 2006; Zhang et al. 2008), and such bacterial communities may be involved in the degradation of intermediate products of the fungal decomposition (de Boer et al. 2005; Frey-Klett et al. 2011). Recently, bacteria from the fungal decay environment of the white-rot fungus *Hypholoma fasciculare* have been isolated and their carbon sources were characterised (Valaskova et al. 2009). These acid-tolerant strains were metabolically versatile and could use several low molecular weight sugars that are potentially released by extracellular fungal cellulases and hemicellulases of the fungus (Valaskova et al. 2009). Moreover, Voro'ev et al. (2009) have isolated methylotrophic microorganisms from beech wood blocks incubated on the surface of an acidic forest soil during wood decay by the white-rot fungus *H. fasciculare* (Voro'ev et al. 2009). These obligatory acidophilic, facultative methylotrophic microorganisms are proposed as new genus *Methylovirgula ligni* and can endure pH values less than 3.5 (Voro'ev et al. 2009). Such acidophilic bacteria with carbon source independency may occur by chance in fungal environments or are actively integrated in the process of fungal wood decay via the release of methanol during lignin degradation (De Boer and van der Wal 2008). In addition, members of the phylum *Verrucomicrobia* have been detected in tree logs (Zhang et al. 2008), and representatives of this phylum have also been characterised as acidophilic methanotrophs (Dunfield et al. 2007). Potential methylotrophic bacteria such as members of the genera *Xanthobacter* and *Mycobacterium* (Kolb 2009) were found in wood chip piles indicating that methanol released during wood decomposition was present.

Moreover, Kulichevskaya et al. (2011) described in detail an acidobacterial strain of the proposed new genus *Acidicapsa ligni*, which was isolated from the same environment. *A. ligni* were strictly aerobic and acidophilic mesophiles and preferred sugars as growth substrates (Kulichevskaya et al. 2011). Interestingly, close relatives of this genus have been found in high relative abundances in the late stage of storage of a wood chip pile (Noll et al. 2010b) and affiliated sequences to these phyla were also obtained in green waste and tree logs (Adams and Frostick 2009; Zhang et al. 2008) and preserved wood (Jakobs-Schönwandt et al. 2010).

Limitations for microbial decomposition in stored woody biomass

In forest ecosystems, both trees and microbial growth are limited by the abundance of macro- and microelements (Cowling and Merrill 1966; Spano et al. 1982; Weedon et al. 2009). For the majority of brown-rot and some white-rot fungi are bio-available, Fe compounds essential to mediate the non-enzymatic Fenton reaction (Arantes and Milagres 2007). Iron species are present in wood mainly as iron oxy(hydr)oxide, which is reduced and solubilized by specific fungal mechanisms (Arantes et al. 2011). Details of the Fenton reaction are still in discussion and the minimal amount of Fe mandatory to perform the Fenton reaction is related to many factors such as the composition of macromolecules in wood, the oxidation status of Fe in wood, the pH in wood, the fungal ability to create siderophores, other enzymatic options of the fungi and many more. Much research on the Fenton reaction has been carried out by employing the model brown-rot fungi *Gloeophyllum trabeum*. *G. trabeum* degraded cellulose much better in low-iron concentrations compared to high-iron concentrations (Xu and Goodell 2001) indicating that the fungi is highly adapted to a low-iron-containing environment such as wood.

Much research has been carried out in nitrogen limitations in ecosystems (Elser et al. 2000), and recently such limitations for fungal and fungal–bacterial wood decay have been reported (Weißhaupt et al. 2011, 2012). Similarly, these findings are applicable for the microbial decomposition processes inside wood chip piles.

Nitrogen is expected to limit decomposition because the degrading enzymes needed for wood decay are nitrogen-rich, with C/N ratios of ~3:1 (Sterner and Elser 2002), far narrower than wood ratios of 200–1,200:1. As a result, the immobilisation and accumulation of nitrogen during the decomposition process (Busse 1994), the fixation of atmospheric N_2 (Jurgensen et al. 1989), the capture of nitrogen from atmospheric deposition (Kuehne et al. 2008), possibly the re-translocation of nitrogen through extensive fungal hyphae (Tlalka et al. 2008), and degradation of present microbial biomass by fungi (Fermor and Wood 1981; Weißhaupt et al. 2012) are important processes to reduce nitrogen limitation for fungi and accelerate wood decomposition. As the concentration of nitrogen in wood is very low (Weißhaupt et al. 2011) and the bioavailability of nitrogen derived of atmospheric deposition is also low, fixation of atmospheric N_2 is a reasonable additional nitrogen source for the wood-decomposing community (Granhall and Lindberg 1978; Hendrickson 1991; Jurgensen et al. 1989). Several studies have noted a relationship between nitrogen fixation rates in woody debris and temperature, moisture or oxygen concentration (Sharp 1975; Silvester 1989; Sollins et al. 1987; Hicks et al. 2003). Members of the genera *Pseudomonas* and *Rahnella* were discovered in pine wood chip piles and tree logs, respectively (Noll et al. 2010b; Zhang et al. 2008), and these genera have been previously characterised as diazotrophs (Kim et al. 1997; Yan et al. 2008). Moreover, members of the diazotrophic genera *Azoarcus*, *Bradyrhizobium*, *Burkholderia*, *Frankia* and *Xanthobacter* (Urakami et al. 1995; Kaneko et al. 2002; Bevivino et al. 1994; Callaham et al. 1978) were found in similar environments (Zhang et al. 2008; Novinscak et al. 2009; Adams and Frostick 2009) suggesting that the ability for diazotrophic activity is advantageous in wood-decomposing environments. In contrast, members of the genera *Pseudoxanthomonas* and *Thauera* were found in composted biosolids (Novinscak et al. 2009), which are able to perform denitrification processes (Chen et al. 2002; Mechichi et al. 2002). If such bacterial denitrification processes take place at in situ conditions, then nitrate is bio-available and nitrogen availability might not be the key limitation for microbial activity in wood decomposition.

In addition, limitations for microbial wood decomposition may also be related to the bioavailability of sulphur. Sulphur sources such as air pollution have decreased significantly across Europe and North America leading to limiting terrestrial environments (McGrath and Zhao 1995) and wood is almost free of sulphur (Struis et al. 2008). The main preferred sulphur species for plants, bacteria and fungi is sulphate. However, wood-decomposing basidiomycetes are able to utilise even traces of sulphur in wood and transform it to sulphate-ester and thiol biomass structure (Schmalenberger et al. 2011). In addition, close relatives to the genus *Thioalkalivibrio* and *Thiobacillus* were detected in composted biosolids (Novinscak et al. 2009), and members of both genera were able to oxidise a number of sulphur species such as thiosulfate, sulphide and elemental sulphur (Sorokin et al. 2001).

Microbial activity as catalyser of self-ignition processes in stored woody biomass

The role of microbial activity as one of the most important factors in initiating heat development which can lead to self-ignition in large chip piles has been frequently studied (Springer and Hajny 1970; Kubler 1987). The distribution and the type of microbial community at different zones of a large pile are largely determined by the zone temperature. Bergman and Nilsson (1974) reported that low temperature areas were mainly dominated by blue-stain fungi while moderate temperature facilitated the growth of basidiomycetes, moulds, *Sporotrichum pulverulentum* (syn. *Chrysosporium lignorum*) and *Allescheria terrestris*. Maximum temperature for the growth of the majority of decay fungi (mesophilic) is between 30 and 40 °C while thermophilic fungi can tolerate temperatures up to 60 °C (Nilsson 1965).

Self-ignition of wood chip piles occurs when the heat production inside the pile is higher than its heat release rate. Heat generation, caused by a combination of variable impacts of microbial activities (i.e. respiration), slow oxidative reactions and physical processes, leads to exponentially increasing temperatures which can end up in self-ignition (Ferrero et al. 2011). Self-ignition processes in wood chip piles was modelled and thereafter concluded that critical temperatures were only feasible when the initial heat was generated by microbial activity (Ferrero et al. 2009; see also Fig. 2).

Due to increasing temperature inside wood chip piles, the presence of thermophilic microorganisms is dominating while other types are limited in such environments (Scholz et al. 2005). Therefore, after a temperature change, a shift in the community composition and function is reasonable as frequently demonstrated in other environments (Conrad et al. 2009; Noll et al. 2010a). Thermophilic microorganisms have been frequently found in wood chip piles, where increased temperatures have been recorded (Novinscak et al. 2009; Adams and Frostick 2009; Scholz et al. 2005). This correlation of temperature and shift in microbial diversity suggests that in situ temperature will be of high importance not only for the microbial composition but also for its

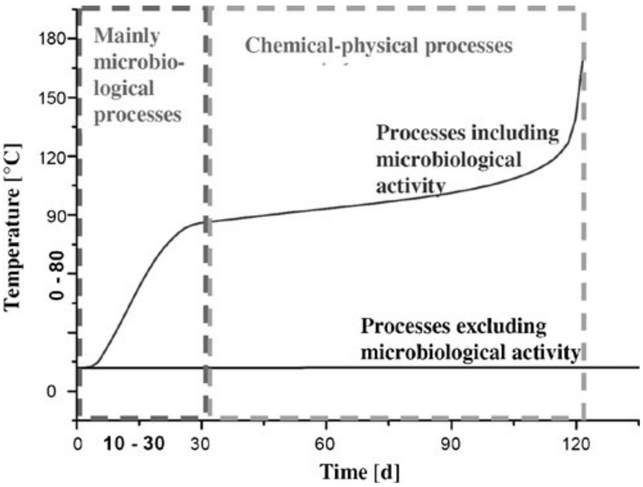

Fig. 2 Potential temperature evolutions in wood chip piles with and without microbial activity

functioning. After optimal temperature for respective microorganisms is exceeded, microbial activity will decrease to maintenance metabolism and outcompeted by more thermophilic microorganisms. Although few microorganisms can cope with high temperatures up to 110 °C (Schönheit and Schäfer 1995), the overall microbial activity and in particular the wood decomposition activity will decrease in wood chip piles already at temperatures above 80 °C (Ferrero et al. 2009).

Health risks by the microbial community in stored woody biomass

Pulmonary inflammation in persons working close to wood chip piles have been frequently reported (Wintermeyer et al. 1997; Määttä et al. 2006), and pathogenic fungi (e.g. *Candida*, *Aspergillus*, *Mucoraceae*, *Geotrichum*) and bacteria (e.g. *Aeromonas*) have been reported in environments of stored woody biomass (see Table 1). Members of the genera *Candida* and *Aspergillus* are epidemoligically the most common causes of invasive fungal infections (Richardson and Lass-Flörl 2008). *Candida* spp. may cause a spectrum of diseases, ranging from thrush to invasive diseases such as arthritis, osteomyelitis, endocarditis, endophthalmitis, meningitis or fungemia (Fridkin and Jarvis 1996). Members of the genus *Aspergillus* are known to be both saprophytes commonly grow on decaying plant material and important air-borne fungal pathogens causing invasive and non-invasive pulmonary infections or allergic bronchopulmonary aspergillosis (Mccormick et al. 2010). Pathogenic representatives of the genus *Aeromonas* are described to cause hemolytic uremic syndrome, burn-associated sepsis, and a variety of respiratory tract infections, including epiglottitis (Janda and Abbott 1998). Moreover, members of the same bacterial genus have been found in soil environments to be able to degrade cellobiose and glucose at anoxic conditions (Schellenberger et al. 2010), indicating that they are also involved in wood decomposition processes. Members of the fungal family *Mucoraceae* are able to cause severe mycosis (Ribes et al. 2000). However, illness by fungal pathogens in particular by *Mucoraceae* is more likely in immunosuppressive persons (e.g. diabetes, HIV, leukaemia, lymphoma, transplantation patients) as these fungi are predominantly opportunists when causing human disease (Ribes et al. 2000). However, other opportunistic yeast-like fungi and moulds such as *Zygomycetes*, *Fusarium* spp. and *Scedosporium* spp. are also found in wood chip piles (Lindner et al. 2011; Noll et al. 2010b; Hansgate et al. 2005) and are increasingly being recognised in patient groups such as those with leukaemia and in bone marrow transplant recipients (Richardson and Lass-Flörl 2008).

For this reason, the level of safety procedures for handling stored woody biomass and its dust, which can contain high concentrations of hazardous microorganisms (Sebastian et al. 2006), should be recognised and included in standard procedures worldwide. In addition, security procedures in the handling of wood chips should be established and continuously audited as already lethal injuries of workers occasionally occurred (Furumiya et al. 2011).

Conclusions

In the context of microbial ecology in wood chip piles and their impact on the wood quality as fuel, more studies are needed to better understand which microorganisms are actively decomposing wood chips, which environmental conditions enhance microbial degradation and finally how storage conditions in and outside of forest environments can be optimised to reduce loss of fuel quality by microbial activity.

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